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A subtribal classification of Malesian and Southwest Pacific woody bamboos (Poaceae: Bambusoideae: Bambuseae) informed by morphological and molecular studies

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Summary. From the accruing indications of recent morphological and molecular studies, it is possible to recognize seven major lineages corresponding to distinct subtribes of woody bamboos for the Malesian–Southwest Pacific region. A key to the subtribes is presented, providing morphological distinctions to reflect synapomorphic or putatively synapomorphic character-states defining the lineages. Besides the Bambusinae and Melocanninae, four subtribes are newly recognized and the concept of Racemobambosinae is emended. The newly circumscribed subtribes include Dinochloinae, Greslaniinae, Holttumochloinae, and Temburongiinae. Notes are provided for a small number of taxa of uncertain subtribal position. With the exception of the Bambusinae, in which genera are known to form an introgressive complex, the constituent genera of the other subtribes in Malesia and the Southwest Pacific are also keyed out.

This paper is dedicated to our colleague Dr Soejatmi Dransfield for her insightful work on Malesian and Madagascan bamboos on the occasion of her 77th birthday.

BACKGROUND AND SCOPE OF THE PRESENT WORK

The most recent classifications of bamboos recognize three major lineages, the temperate woody bamboos (Arundinarieae), tropical woody bamboos (Bambuseae) and herbaceous bamboos (Olyreae) (Sungkaew et al. 2009, BPG 2012, Clark et al. 2015). The tropical woody bamboos, including 942 species (411 neotropical, 531 paleotropical) (Vorontsova et al., in press), currently appear to be the biggest tribe, within which two geographically distinct subgroups, the Paleotropical and Neotropical woody bamboos, are apparent (Sungkaew et al. 2009). Tropical woody bamboos are almost universally tetraploids or hexaploids, while temperate bamboos are characteristically tetraploids, and herbaceous bamboos diploids (Soderstrom 1981, Judziewicz et al. 1999, BPG 2012).

The Bamboo Phylogeny Group (BPG 2012) has reviewed the classification of tribes and subtribes, summarizing and discussing the morphological features that help define many of these groups, but it was recognized that refinements are still required in a number of cases. More recently completed work, such as the use of information from multiple chloroplast regions, is expected to further inform on these relationships, especially among both Paleotropical and Neotropical bamboos (Chokthaweepanich 2014).

Meanwhile, the subtribal classification of Paleotropical bamboos remains highly unsatisfactory. Four subtribes are currently recognized: Bambusinae, Melocanninae, Hickeliinae, and Racemobambosinae (BPG 2012, Kellogg 2015). Of these, the Melocanninae have consistently been a well-supported monophyletic group in molecular analyses of moderate to large datasets (Yang et al. 2008, Sungkaew et al. 2009, Goh et al. 2013, Chokthaweepanich

2014, Goh et al., unpublished), although some internal (generic) relationships still require clarification, but the other three subtribes have had uncertain delimitation.

The analyses of Sungkaew et al. (2009), Goh et al. (2010, 2013) and Chokthaweepanich (2014) have individually demonstrated a number of clades and less well-supported clusters of genera external to the main Bambusinae using different combinations of molecular markers, without accomplishing totally conclusive resolution throughout. The main introgressing complex formed by *Bambusa* Schreber, *Dendrocalamus* Nees and *Gigantochloa* Kurz ex Munro and their allies such as *Maclurochloa* K.M.Wong, *Melocalamus* Benth., *Phuphanochloa* Sungkaew & Teerawat., *Soejatmia* K.M.Wong, and *Thyrsostachys* Gamble, referred to as the BDG complex of the Bambusinae by Goh et al. (2013), had a contentious relationship with a clade sister to it formed by *Holttumochloa* K.M.Wong and *Kinabaluchloa* K.M.Wong (Goh et al. 2010, 2013; Chokthaweepanich 2014) and these were more phylogenetically distinct from other groups, including the Racemobambosinae. Sungkaew et al. (2009) also demonstrated the inclusion of *Vietnamosasa* Nguyen within the Bambusinae. There were, meanwhile, other consistently recovered isolated lineages such as *Temburongia* S.Dransf. & K.M.Wong, and a cluster comprising the climbing-scrambling genera *Dinochloa* Buse, *Mullerochloa* K.M.Wong and *Sphaerobambos* S.Dransf. together with the erect to clambering *Neololeba* Widjaja, or the 'DMNS clade' (Goh et al. 2013). Such studies (including Chokthaweepanich 2014, Goh et al. unpublished), sampling even more taxa, have begun to reveal a rich diversity of associations external to the Bambusinae and excluded from the somewhat clearer definitions of Racemobambosinae and Hickeliinae.

The Hickeliinae were still considered to include not only *Hickelia* A.Camus and allies from the Madagascar–Réunion region, but also other taxa from Indonesia and Papua New Guinea in the Malesian region placed in *Nastus* Juss. (BPG 2012). However, more recent analyses (Chokthaweepanich 2014, Goh et al. unpublished) have begun to affirm that the Malesian species of *Nastus* have been clearly misplaced in that genus. The species of *Nastus* from the Madagascar–Réunion region also need further clarification, as they are still very little understood (Dransfield, pers. comm.) but Wong & Dransfield (2016) have shown that the misplaced Malesian taxa form three distinct genera, *Chloothamnus* Buse, *Ruhooglandia* S.Dransf. & K.M.Wong and *Widjajachloa* K.M.Wong & S.Dransf.

It is an understatement to say that the classification of the Paleotropical bamboos, or for that matter, all of the subfamily Bambusoideae, has been particularly problematic. It seems certain now that only with a great deal more effort in taxon sampling and a more comprehensive inclusion of gene regions, both plastid and nuclear, can unambiguous topologies of molecular phylogenetic analyses across the Paleotropical bamboos be expected, and our understanding of relationships dramatically improve. Furthermore, the Malesian–Southwest Pacific region holds a rich diversity of genera of which many taxa are still incompletely represented in specimen material, so that an adequate summary of relationships can only benefit from better understanding the molecular relationships revealed in the various studies, advancing our survey and documentation of morphological attributes, and exploring the association

between these and morphological characteristics unique to individual groups and clusters of taxa. In this contribution based on such a collective approach, we outline a system of subtribal delimitation for Paleotropical bamboos in the Malesian–Southwest Pacific region, where clearly the continued retention of three existing subtribes (Bambusinae, Melocanninae, Racemobambosinae) and a misapplied subtribe (Hickeliinae) is highly unsatisfactory for indicating the most likely relationships.

We present first a key to the subtribes thought to be most feasible based on the available indications from various lines of evidence, both molecular and morphological. The genera within subtribes are also keyed out, except in the Bambusinae, which mainly includes an introgressive complex that needs greater taxonomic elucidation. Following this, the subtribes are enumerated and the attendant underlying premises for their recognition are discussed.

KEY TO MALESIAN–SOUTHWEST PACIFIC BAMBOO SUBTRIBES AND GENERA

1A. Ovary apex gradually narrowed into a stiff hollow style with a central tissue strand (**5.** Subtribe **MELOCANNINAE**) ..... ***Schizostachyum***

1B. Ovary apex abruptly narrowed into a soft flexuous, tissue-filled style, or without a conspicuous style,

2A. Auricles on culm leaf sheaths and foliage leaf sheaths horn-like (typically narrow and stiffly erect), patella present as a thin, plate-like extension around culm nodes (**7.** Subtribe **TEMBURONGIINAE**),

3A. Inflorescences indeterminate, with pseudospikelets in clear clusters of several to many (Luzon Is. in Philippines, South Sulawesi, East Java, Alor (Lesser Sunda Islands), New Guinea) ..... ***Fimbribambusa***

3B. Inflorescences ‘determinate’ (probably an extreme reduction of the indeterminate condition), with spikelets solitary or in sparse clusters (NW Borneo) ..... ***Temburongia***

2B. Auricles on culm leaf sheaths and foliage leaf sheaths indistinct or low, to lobe-like, but not horn-like; patella not present,

4A. Inflorescence indeterminate, with pseudospikelets,

5A. Midculm branch complement with a clearly dominant primary axis,

6A. Base of the culm leaf sheath smooth, not rugose or wrinkled (**1.** Subtribe **BAMBUSINAE**),

6B. Base of the culm leaf sheath transversely wrinkled (‘rugose’),

7A. Rudimentary florets (with only lemma and reduced palea developed) present, 1–2, between glumes and perfect (fertile) florets in the pseudospikelet (**1A.** Possibly introgressed member of Subtribe **BAMBUSINAE**) ..... ***Soejatmia***

7B. Rudimentary florets not occurring below perfect florets (**2.** Subtribe **DINOCHLOINAE**),

8A. Only 1 perfect floret in the pseudospikelet; paleas not keeled,

9A. Culms twining; culm internodes basally distended; style glabrous ..... ***Dinochloa***

9B. Culms suberect-scrambling; culm internodes not basally distended; style hairy ..... ***Cyrtochloa***

8B. More than 1 perfect floret in the pseudospikelet; paleas 2-keeled,

10A. Lodicules present, culm internodes basally distended; stamens 4; filaments fused into a tube ..... ***Mullerochloa***

10B. Lodicules absent, culm internodes not basally distended; stamens 6, filaments free,

11A. Paleas longer than lemmas, the keels winged ..... ***Sphaerobambos***

11B. Paleas shorter than, or as long as, lemmas, the keels without wings,

12A. Pseudospikelets flat or compressed, the glumes and lemmas spreading outwards at the apices; lemma apices short-cuspidate ..... ***Neololeba***

12B. Pseudospikelets subterete, the glumes and lemmas closely appressed; lemma apices long-setiform,

13A. Pseudospikelets 25–52 mm long; culm leaf sheath margin papery ..... ***Parabambusa***

13B. Pseudospikelets 4–5 mm long; culm leaf sheath margin firm ..... ***Pinga***

5B. Midculm branch complement without a clearly dominant primary element, all branches subequal (**4.** Subtribe **HOLTTUMOCHLOINAE**),

14A. Midculm branch complement developing from several to many distinct buds ..... ***Holttumochloa***

14B. Midculm branch complement developing from a single bud .... ***Kinabaluchloa***

4B. Inflorescences determinate, with spikelets,

15A. Inflorescence branches subtended by well-developed prophylls or bracts

16A. Culms suberect to erect, unbranched or with solitary branches (these branched again away from their base); base of leaf sheaths and topmost part of branch internodes glabrous; glumes and lemma glabrous on the back (**3.** Subtribe **GRESLANIINAE**) ..... ***Greslania***

16B. Culms scrambling to climbing, with primary branches that rebranch to several orders at their base; base of leaf sheaths and topmost part of branch internodes with rigid retrorse hairs; glumes and lemma conspicuously brown-hairy all over the back ..... ***Ruhooglandia*** (Subtribal position uncertain)

15B. Inflorescence without branches, or branches without prophylls or bracts,

17A. Spikelet with 2 glumes ..... (Subtribal position uncertain: several Malesian taxa currently named as *Racemobambos*; also *Temochloa* from Thailand)

17B. Spikelet with 3–5 glumes (**6.** Subtribe **RACEMOBAMBOSINAE**),

18A. Primary axis of branch complement elongating first or contemporaneously with the 2–several higher-order branches from its base, all similar in size and rebranching distally (Java, Wallacea, New Guinea) .... ***Chloothamnus***

18B. Primary axis of branch complement at lower and middle culm nodes initially dormant, much bigger than the short and slender higher-order branches developing first from its base, these higher-order branches not rebranching away from their base,

19A. Spikelet with 3–8 perfect florets; branch bud and branch complement at or above the culm nodal level ..... ***Racemobambos***

19B. Spikelet with 1 perfect floret; branch bud and branch complement dipping below the culm nodal level ..... ***Widjajachloa***

SYNOPTIC ENUMERATION OF SUBTRIBES IN THE MALESIAN–SOUTHWEST PACIFIC REGION

1. BAMBUSINAE J.S.Presl in K.B. Presl, Rel. Haenk. 1 (1830) 256.
TYPE: *Bambusa* Schreb.

Diagnostic characters:
Leptomorph rhizomes lacking. Culm bases sympodial, necks short to elongated. Culm nodes without patella. Aerial branching well-developed; mid-culm branch complement derived from a solitary primary bud, typically with the primary branch dominant in size and length, 1–few subdominants from its base, and smaller higher-order branches from these axes, rarely with reduction to just a solitary branch; the primary branch axis rarely (e.g., *Maclurochloa*, *Melocalamus*) elongating to reiterate the culm, rebranching distally; thorns absent or (in some *Bambusa*) present. Culm leaves well developed, often bearing fimbriae or fimbriate auricles or not (sometimes glabrous) at the sheath summit; oral setae present or absent; sheath base without transverse wrinkles (except in *Soejatmia*: see 1A below). Foliage leaf sheaths with fimbriae or fimbriate auricles or not at the summit. Synflorescences indeterminate (pseudospikelets), paniculate. Spikelets proper of the pseudospikelets consisting of (0) 1–several glumes, 1–10 or more perfect (fertile) florets, sometimes with 1–3 terminal rudimentary florets. Palea with wingless keels, rarely without keels. Stamens 6, filaments free or fused. Ovary glabrous with hairy apex, with a long slender, flexuous, tissue-filled style; stigmas 1, 2 or 3. Caryopsis basic or (in *Melocalamus*) baccate.

(Fig. 1–3)

Distribution: India to South China, across Indochina, Malesia to northern Australia and the Southwest Pacific.
Malesian genera: *Bambusa* Schreber, *Dendrocalamus* Nees, *Gigantochloa* Kurz ex Munro, *Maclurochloa* K.M.Wong
Extra-Malesian genera: *Melocalamus* Benth., *Oreobambos* K.Schumann, *Oxytenanthera* Munro, *Phuphanochloa* Sungkaew & Teerawat., *Pseudoxytenanthera* Soderstr. & Ellis, *Thyrsostachys* Gamble, *Vietnamosasa* Nguyen.

Comments: The BDG is now shown to be an introgressive complex by Goh et al. (2013), and the inclusion of the above genera in a well-supported Bambusinae clade is clear through the work of Sungkaew et al. (2009), Goh et al. (2011, 2013) and Chokthaweepanich (2014). There will be a need to recognize further intermediate taxa (such as ×*Gigantocalamus* K.M.Wong) (Goh et al. 2011) as well as those that have outstandingly diagnostic morphological characters (such as *Maclurochloa*, *Phuphanochloa*) in this complex/subtribe.

1A. ***Possibly introgressed member of Subtribe Bambusinae (Soejatmia)***
The position of *Soejatmia* K.M.Wong is clearly within the introgressive complex of the Bambusinae (Goh et al. 2013). Yet this remains the only 'odd' genus of the BDG complex

Fig. 1. In the Bambusinae, the primary branch is typically dominant in size and length, with 1–few subdominants from its base, and smaller higher-order branches from these axes (**A**, *Bambusa gurgandii*; **B**, *Dendrocalamus pendulus* with especially elongated primary branches). Sometimes the primary axis remains dormant at first with development of smaller higher-order branches from its base (**C**, *Melocalamus compactiflorus*; **D**, *Maclurochloa*, culm on right), but this later develops into a large branch that reiterates the parent culm in length and size (**D**, culm at top left), extending the shoot system and granting an effective clambering habit. The primary branch axes rebranch distally (shown only for **B**). (Photos: K.M. Wong)

Fig. 2. *Gigantochloa levis* and many other (but certainly not all) species of Bambusinae are large, even imposing, erect-suberect species. Among Southeast Asian bamboos, several taxa in the Melocanninae are also similarly large erect bamboos. (Photo: M. Sugumaran)

Fig. 3. Indeterminate inflorescence development with pseudospikelets that keep proliferating from buds at their base to produce higher-order pseudospikelets, resulting in the pseudospikelet tufts seen in the Bambusinae (**A**, unnamed member of the 'BDG' introgressive complex formed among *Bambusa*, *Dendrocalamus* and *Gigantochloa*), Dinochloinae, Holttumochloinae, Melocanninae (**B**, *Schizostachyum blumei*), and part of Temburongiinae. (Photos: K.M. Wong)

that has the transverse wrinkles at the culm leaf sheath base, which otherwise is a neat synapomorphy for the Dinochloinae. The possibility of inter-subtribal gene capture cannot be ruled out, as this has been demonstrated to occur among grass tribes (Mason-Gamer 2004). *Soejatmia* has rudimentary florets occurring below perfect florets, which is not known in the other SE Asian – Pacific bamboos here, except in *Temburongia* S.Dransf. & K.M.Wong; it is possible that this feature simply represents an uncommon peculiarity during complex evolution, as the inflorescence in *Temburongia* seems intermediate between the semelauctant and iterauctant conditions (see comments under Temburongiinae).

2. DINOCHLOINAE K.M.Wong & W.L.Goh, **subtribus novum**

The new subtribe Dinochloinae is distinctive among Paleotropical bamboos in having culm-sheath bases which are transversely wrinkled; culm nodes not developing a patella; a mid-culm branch complement with a clearly dominant axis; indeterminate inflorescences; no rudimentary florets below the perfect florets; and a flexuous tissue-filled style.
TYPE: *Dinochloa* Büse

Diagnostic characters:
Leptomorph rhizomes lacking. Culm bases sympodial, necks short to elongated. Culm nodes without patella. Aerial branching well-developed; mid-culm (or upper culm) branch complement derived from a solitary primary bud, typically with the primary branch dominant in size and length over smaller higher-order branches that may develop from its base; the primary branch axis sometimes dormant at first but elongating to reiterate the culm, rebranching distally (but sometimes not, as in some *Neololeba* and *Parabambusa*); thorns absent. Culm leaves well developed, bearing fimbriae or fimbriate auricles or not at the sheath summit; oral setae absent or present; sheath base with a distinctive zone of transverse wrinkles. Foliage leaf sheaths with fimbriae or fimbriate auricles or not at the sheath summit. Synflorescences indeterminate (pseudospikelets), paniculate. Spikelets consisting of 1–3 glumes, 1 (*Dinochloa*), 3–5 (*Sphaerobambos*), 3–12 (*Neololeba*, *Parabambusa*) perfect (fertile) florets, with a terminal rudimentary floret or (*Cyrtochloa*) without. Palea not keeled or keels winged (*Sphaerobambos*) or wingless. Stamens 4 or 6, filaments free. Ovary glabrous or hairy at summit, with a short or elongate flexuous and tissue-filled style; stigmas 1–3. Caryopsis basic or (in *Cyrtochloa*, *Dinochloa*, *Sphaerobambos*) baccate.

(Fig. 4–5)

Distribution: Andamans, South Thailand, Malesia, Queensland.
Malesian genera: *Cyrtochloa* S.Dransf., *Dinochoa* Buse, *Neololeba* Widjaja, *Parabambusa* Widjaja, *Pinga* Widjaja, *Sphaerobambos* S.Dransf.
Comments: *Dinochloa* was recovered as a distinct lineage removed from Bambusinae by Yang et al. (2007, 2008). Sungkaew et al. (2009) recovered *Dinochloa* and *Neololeba* in the same clade. The close association of *Dinochloa* and *Sphaerobambos* (Goh et al. 2010),

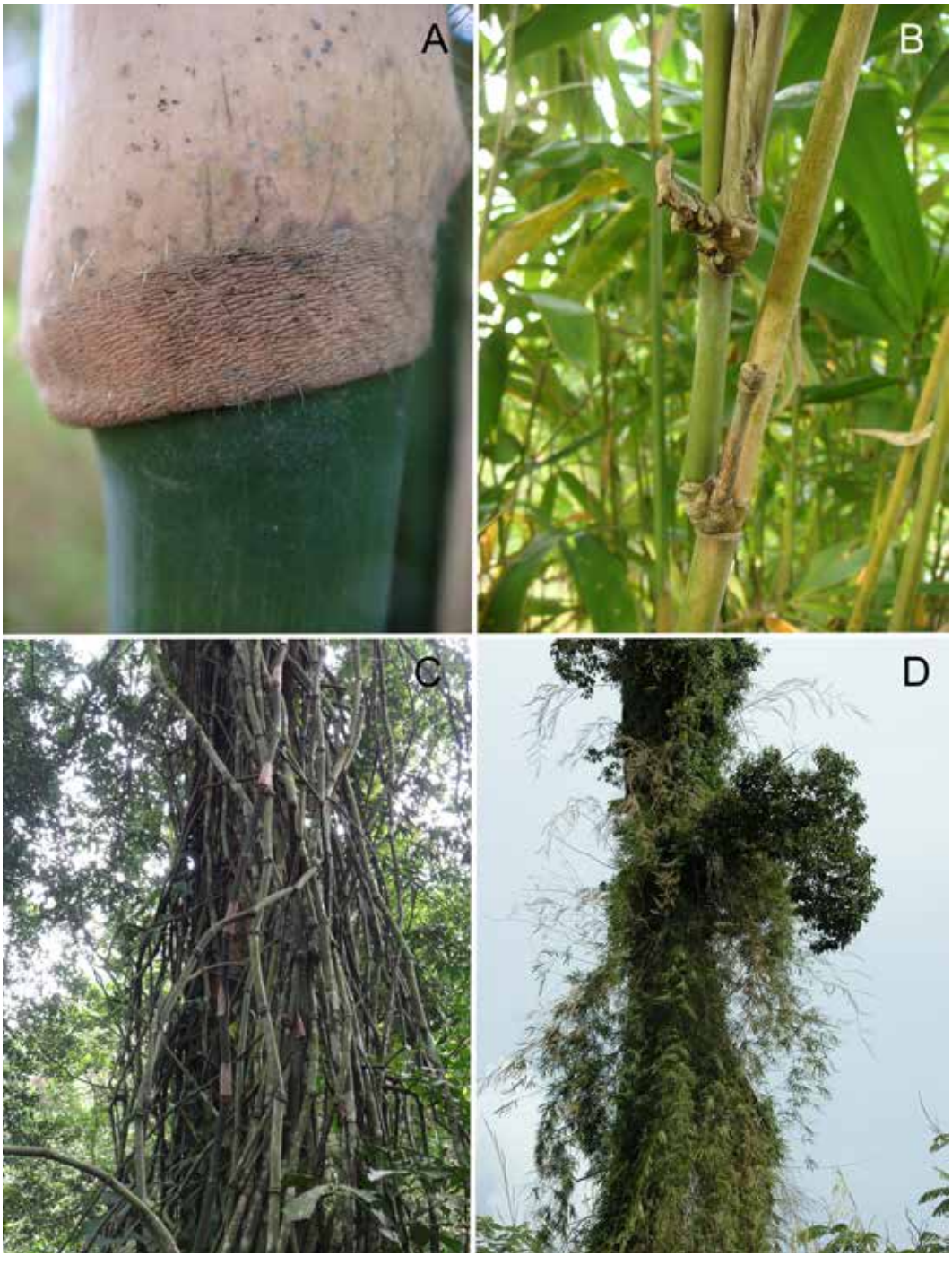

Fig. 4. Dinochloinae: the characteristic, transversely wrinkled culm leaf sheath base (**A**, *Neololeba atra*); typically well-developed aerial branching with the mid-culm (or upper culm) branch complement derived from a solitary primary bud that develops into a primary branch dominant in size and length over smaller higher-order branches from its base (**B**, *N. atra*); reiterative development of such primary branch axes contributes to a clambering or climbing habit (**C**, *Dinochloa scabrida*). In *Dinochloa*, the inflorescences consist of such primary (and initially dormant) branch buds that develop into long, branched flowering axes protruding into clear space away from the foliage thickets (**D**, *D. obclavata*). (Photos: K.M. Wong)

as well as with *Neololeba*, became clearer in molecular experiments reported by Goh et al. (2013). Kelchner et al. (2013) recovered *Neololeba* and *Cyrtochloa* in the same clade. Only in *Dinochloa* are the culms consistently twining. The extra-Malesian *Mullerochloa* has vegetative characteristics compatible with this subtribe, such as clambering and even occasionally twining culms, transverse wrinkles at the culm leaf sheath base, and spikelets with 4–9 glumes, but seems to differ in having stamens with fused filaments. Its inclusion in this subtribe is provisional in view of its consistent position within a clade with *Dinochloa* and allies only in chloroplast-based topologies (Goh et al. 2013, Chokthaweepanich 2014) and not in topologies with nuclear data (Goh et al., unpublished). Only one other genus (*Soejatmia*) outside this tribe is known to have the transversely wrinkled culm leaf sheath base that is otherwise a clear unifying subtribal character for Dinochloinae; however, unlike in that genus, rudimentary florets do not occur below the perfect florets. See comments under *Soejatmia*.

Fig. 5. *Dinochloa scabrida*,cultivated at the Rimba Ilmu Botanical Garden, University of Malaya, showing the extending climbing-clambering shoot system possible through reiterative development of successively higher orders of primary branch axes. (Photo: K.M. Wong)

3. GRESLANIINAE K.M.Wong & W.L.Goh, **subtribus novum**

The new subtribe Greslaniinae is distinctive among Paleotropical bamboos in having erect to suberect culms that are unbranched or with a solitary branch at each branching node; culm nodes not developing a patella; inflorescence branches subtended by distinct prophylls or bracts; and a flexuous tissue-filled style.
TYPE: *Greslania* Balansa

Diagnostic characters:
Leptomorph rhizomes lacking. Culm bases sympodial, necks short. Culm nodes without patella. Aerial branching not developed (*Greslania circinata* Balansa) or just a single branch (*G. rivularis* Balansa) derived from a solitary primary bud, the primary branch not elongating to reiterate the culm, not or seldom rebranching distally; thorns absent. Culm leaves well developed, auricles not developed at the sheath summit; oral setae none; sheath base without a distinctive zone of transverse wrinkles. Foliage leaf sheaths with or without fimbriae at the sheath summit, auricles indistinct. Synflorescences determinate (spikelets), paniculate; inflorescences terminating leafy culms (*G. circinata*) or branches (*G. rivularis*), inflorescence branches subtended by well-developed prophylls or bracts. Spikelets consisting of 2 glumes, 1 perfect (fertile) floret, and a rachilla extension bearing a terminal rudimentary floret. Palea not keeled. Stamens 6, filaments free. Ovary glabrous with hairy summit, style inconspicuous; stigmas 3, arising directly from the ovary summit. Caryopsis basic.
(Fig. 6)

Distribution: Southwest Pacific: New Caledonia.
Extra-Malesian genera: *Greslania* Balansa.
Comments: Recent molecular analyses (Goh et al., unpublished) show *Greslania* as an independent clade. The molecular phylogeny by Chokthaweepanich (2014) shows *Greslania* to be a distinct clade closer to the Dinochloinae than to the Racemobambosinae. The morphological analysis of two species by Dransfield (2002) adds to that by McClure (1966).

4. HOLTTUMOCHLOINAE K.M.Wong & W.L.Goh, **subtribus novum**

The new subtribe Holttumochloinae is distinctive among Paleotropical bamboos in having culm nodes not developing a patella; mid-culm branching without any dominant axis and all branches subequal; indeterminate inflorescences; and a flexuous tissue-filled style.
TYPE: *Holttumochloa* K.M.Wong

Diagnostic characters:
Leptomorph rhizomes lacking. Culm bases sympodial, necks short. Culm nodes without patella. Aerial branching well-developed; mid-culm branch complement derived from a solitary primary bud or (in *Holttumochloa*) a complement of several to numerous small

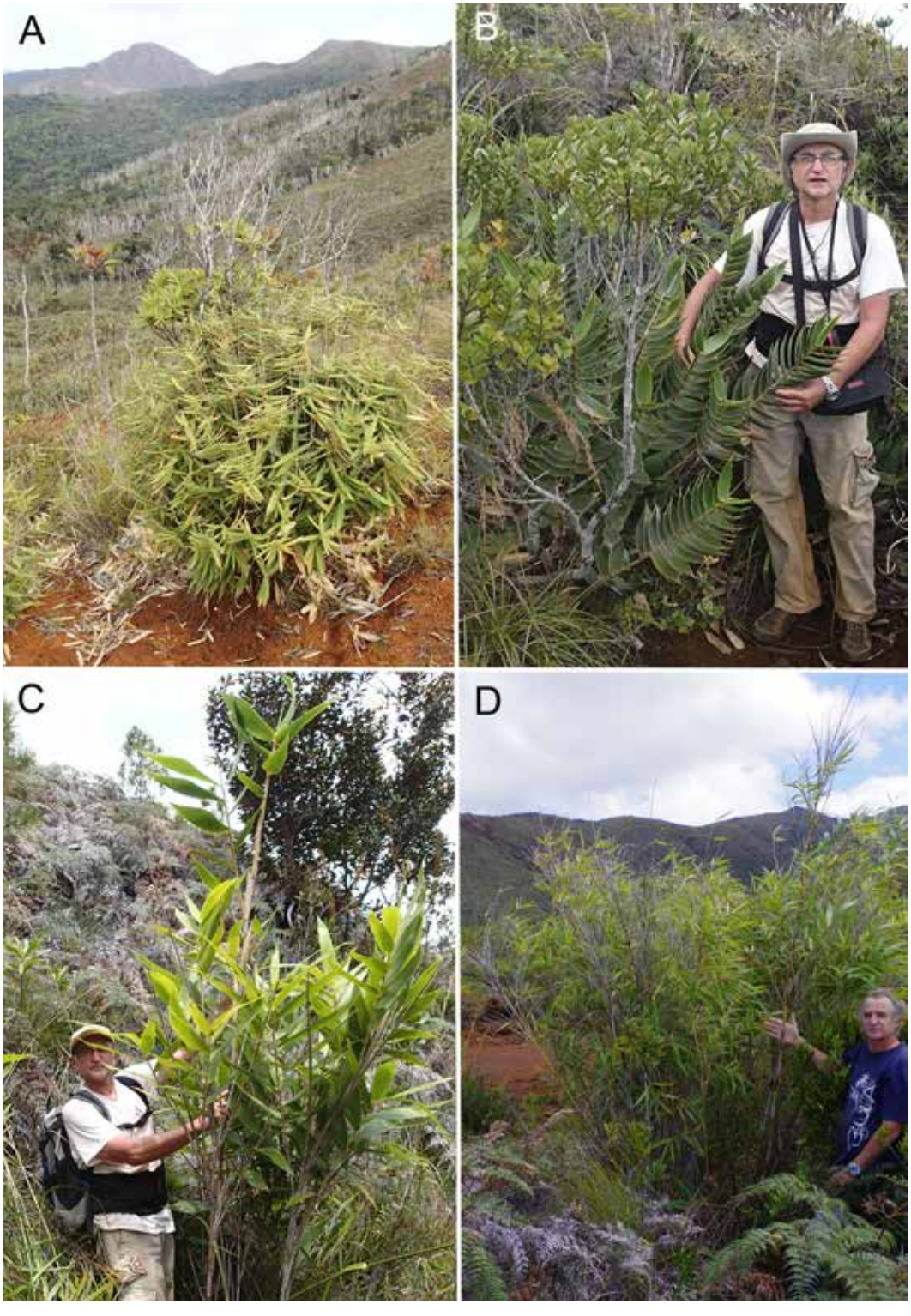

Fig. 6. Greslaniinae: unbranched culms in *Greslania circinata* (**A**) and *G. montana* (**B**, with Robert Kernin), or culms producing only solitary branches (**C**, *G. rivularis*), these sometimes repeatedly producing solitary branches sufficiently to give a bushy appearance (**D**). (Photos: Robert Kernin)

primary buds, all branches typically slender and subequal, the primary branch(es) none dominant and not elongating to reiterate the culm, not or seldom rebranching distally; thorns absent. Culm leaves well developed, bearing fimbriae or fimbriate auricles or not at the sheath summit; oral setae present or absent; sheath base without a distinctive zone of transverse wrinkles. Foliage leaf sheaths with fimbriae or fimbriate auricles or not at the sheath summit. Synflorescences indeterminate (pseudospikelets), with pseudospikelet clusters along a slender axis or only sparsely paniculately branched. Spikelets consisting of 1–3 glumes, 1–3 perfect (fertile) florets, and a terminal rudimentary floret. Palea not keeled or keels wingless. Stamens 6, filaments free. Ovary glabrous with hairy summit, style inconspicuous; stigmas 3, arising directly from ovary summit. Caryopsis basic.

(Fig. 7)

Distribution: Mainland SE Asia, Malay Peninsula, NW Borneo.
Malesian genera: *Holttumochloa* is known only in Thailand and the Malay Peninsula. *Kinabaluchloa* K.M.Wong straddles the South China Sea with two species, one in mainland SE Asia (Vietnam to north Malay Peninsula), the other in NW Borneo.
Extra-Malesian genera: *Nianhochloa* H.N.Nguyen & V.T.Tran is not known in Malesia, only in the highlands of Vietnam.
Comments: *Holttumochloa* and *Kinabaluchloa* have been recovered as a clade external to the main Bambusinae (BDG complex) by Goh et al. (2010, 2013) and Chokthaweepanich (2014). Our analyses (Goh et al., unpublished) show *Nianhochloa* to cluster with *Kinabaluchloa* and *Holttumochloa*. As shown in the key, the morphology between *Holttumochloa* and *Kinabaluchloa* would seem rather contrasting. However, it would seem practical to keep them in a single subtribe, rather than have two or three, as suggested by their molecular relationship. In Yang et al. (2008) the extra-Malesian genera *Bonia* Balansa and *Neomicrocalamus* P.C.Keng from China also form a clade just outside Bambusinae. A species earlier misplaced with *Racemobambos* (which typically has determinate inflorescences) (Chao & Renvoize 1989) was later restored to *Neomicrocalamus* (*N. prainii* (Gamble) P.C.Keng, with indeterminate inflorescences) (Stapleton 1994, following Keng 1983). The relationship of these genera to either the Bambusinae or Holttumochloinae as here circumscribed is as yet uncertain.

5. MELOCANNINAE Benth., J. Linn. Soc. London 19 (1881) 31.
TYPE: *Melocanna* Trin.
Synonym: Schizostachydinae Soderstr. & R.P.Ellis in Soderstrom et al., Grass Syst. Evol. (1987) 238. TYPE: *Schizostachyum* Nees.

Diagnostic characters:
Leptomorph rhizomes lacking. Culm bases sympodial, necks short to elongated. Culm nodes without patella. Aerial branching well-developed; mid-culm branch complement derived from a solitary primary bud, typically a cluster of subequal branches of various orders

Fig. 7. Branching in Holttumochloinae is characterized by all branches in a complement being typically slender and subequal, which develop from multiple primary buds (**A**, *Holttumochloa magica*) or a solitary primary bud (**B**, **C**, *Kinabaluchloa wrayi*; D, *Nianhochloa*). The primary branch(es) are not dominant and do not elongate to reiterate the culm. (Photos: K.M. Wong)

from the base of the primary axis; the primary branch rarely dominant in size or length and elongating to reiterate the culm (e.g., *Schizostachyum terminale* Holttum), all branches rebranching distally; thorns absent. Culm leaves well developed, often bearing fimbriae or fimbriate auricles at the sheath summit; oral setae present or inconspicuous; sheath base without transverse wrinkles. Foliage leaf sheaths often with fimbriae or fimbriate auricles at the summit. Synflorescences indeterminate (pseudospikelets), paniculate or a capitate cluster terminal to branches. Spikelets proper of the pseudospikelets consisting of 0, 2 or 4 glumes, 1–3 perfect (fertile) florets, with or without rachilla extension bearing a rudimentary floret. Palea keels wingless or winged. Stamens 6 or (in *Ochlandra*) 15–numerous, filaments free or fused. Ovary glabrous, with a long slender, stiff, hollow style with a central tissue strand; stigmas 2 or 3. Caryopsis basic or (in *Melocanna*, *Ochlandra*, *Stapletonia*) baccate, or (in *Pseudostachyum*) nucoid (the pericarp crustaceous).

(Fig. 8)

Distribution: India through South and SE Asia into Malesia and the SW Pacific.
Malesian genera: *Schizostachyum* Nees is the only native Malesian genus of this subtribe.
Extra-Malesian genera: *Cephalostachyum* Munro, *Davidsea* Soderstr & R.P.Ellis, *Dendrochloa* C.E.Parkinson, *Melocanna* Trin., *Ochlandra* Thwaites, *Pseudostachyum* Munro, *Stapletonia* Singh, Dash & Kumari. The mainland SE Asian *Neohouzeaua* A.Camus, including its type species *N. mekongensis* A.Camus and the more recently described *N. fimbriata* S.Dransf., Pattan. & Sungkaew and *N. kerriana* S.Dransf., Pattan. & Sungkaew, have not been distinguishable in molecular analyses. The position of *Teinostachyum* Munro is still contentious, but possibly with *Schizostachyum*. *Annamocalamus* H.N.Nguyen, N.H.Xia & V.T.Tran, another mainland SE Asian genus, probably belongs in this subtribe and is very near *Schizostachyum*, except for its fleshy fruit.
Comments: The Melocanninae are a consistently demonstrable clade (Yang et al. 2007, 2008; Sungkaew et al. 2009, Goh et al. 2013), although *Davidsea*, *Dendrochloa* and *Stapletonia* have not been thus far included in molecular analyses. The occurrence of a conspicuous white-waxy zone or band just below the culm node, easily observed in fresh culms but occasionally sloughed off in very old culms, may also be a distinctive character of this subtribe, although its absence has not been thoroughly demonstrated for members of other Paleotropical woody bamboo subtribes (it also occurs in the neotropical *Chusquea* Kunth).

6. RACEMOBAMBOSINAE Stapleton, **emend.**
TYPE: *Racemobambos* Holttum

Racemobambosinae Stapleton, Edinburgh J. Bot. 51 (1994) 323–324, pro parte, quoad *Racemobambos*, excl. *Vietnamosasa* & *Neomicrocalamus*.

Diagnostic characters:
Leptomorph rhizomes lacking. Culm bases sympodial, necks short. Culm nodes without patella. Aerial branching well developed; mid-culm branch complement derived from a

Fig. 8. Melocanninae taxa typically have florets with a long slender, stiff, hollow style with a central tissue strand, which persists into the fruit stage (**A**, *Schizostachyum lengguanii*), and very frequently the mid-culm branch complement consists of subequal branches of different orders without a dominant axis present (**B**, *S. grande*). (Photos: K.M. Wong)

solitary primary bud, typically a cluster of subequal branches of various orders from the base of the primary axis; the primary branch initially dormant or not, elongating to reiterate the culm or not; all branches seldom or often rebranching distally; thorns absent. Culm leaves well developed, often bearing fimbriae or fimbriate auricles at the sheath summit or not; oral setae present or absent; sheath base without a distinctive zone of transverse wrinkles.
Foliage leaf sheaths often bearing fimbriae or fimbriate auricles or not at the sheath summit. Synflorescences determinate (spikelets), paniculate or not; inflorescence branches not subtended by well-developed prophylls or bracts. Spikelets consisting of 3–5 glumes, 1 (*Chloothamnus*, *Widjajachloa*) or 3–8 (*Racemobambos*) perfect (fertile) florets, with or without a rachilla extension bearing a terminal rudimentary floret. Palea not keeled or keeled and wingless. Stamens 6, filaments free. Ovary glabrous or hairy at summit, style inconspicuous to elongate, flexuous and tissue-filled; stigmas 3, sometimes arising directly from the ovary summit. Caryopsis basic.

(Fig. 9–10)

Distribution: Malesia: Borneo, Sulawesi, Moluccas (Seram Island), Java, Flores, Sumbawa, Sumba, across to New Guinea.
Malesian genera: *Chloothamnus* Buse, *Racemobambos* Holttum, *Widjajachloa* K.M.Wong & S.Dransf.
Comments: *Racemobambos* species allied to the type (*R. gibbsiae* (Stapf) Holttum) have been consistently recovered as a clade distinct from Bambusinae and other clades (Goh et al. 2013). The so-called *Nastus elegantissimus* (Hassk.) Holttum (= *Chloothamnus*) and *N. productus* (Pilg.) Holttum (= *Widjajachloa*) from Indonesia were recovered in the same clade as *Racemobambos* and far removed from *Nastus borbonicus* J.F.Gmel. and *N. elongatus* A.Camus in the Hickeliinae by Chokthaweepanich (2014). The earlier definition of Racemobambosinae by Stapleton (1994) is polyphyletic and both *Vietnamosasa* and *Neomicrocalamus* need to be excluded.

7. TEMBURONGIINAE K.M.Wong, **subtribus novum**

The new subtribe Temburongiinae is distinctive among Paleotropical bamboos by its culm-nodes developing a patella; and its flexuous tissue-filled style.
TYPE: *Temburongia* S.Dransf. & K.M.Wong

Diagnostic characters:
Leptomorph rhizomes lacking. Culm bases sympodial, necks short to elongated. Culm nodes with patella present. Aerial branching well-developed; mid-culm branch complement derived from a solitary primary bud, typically with the primary branch dominant in size and length and smaller higher-order branches from its base; the primary branch bud sometimes dormant at first, then elongating into a dominant axis reiterating the culm in habit and structure, rebranching distally; thorns absent. Culm leaves well developed, often bearing narrow, stiff horn-like auricles, at the sheath summit; oral setae absent; sheath base without transverse

Fig. 9. The Racemobambosinae frequently (not always) have a clambering culm habit (**A**, *Racemobambos gibbsiae*) and are characterized by determinate inflorescences that are either unbranched or sparsely branched (**B**, *R. hepburnii*) or have ebracteate branches, i.e. not subtended by prophylls or bracts (**C**, *Chloothamnus*), and bearing spikelets. (Photos: A & B, Ubaldus Majawal; C, K.M. Wong)

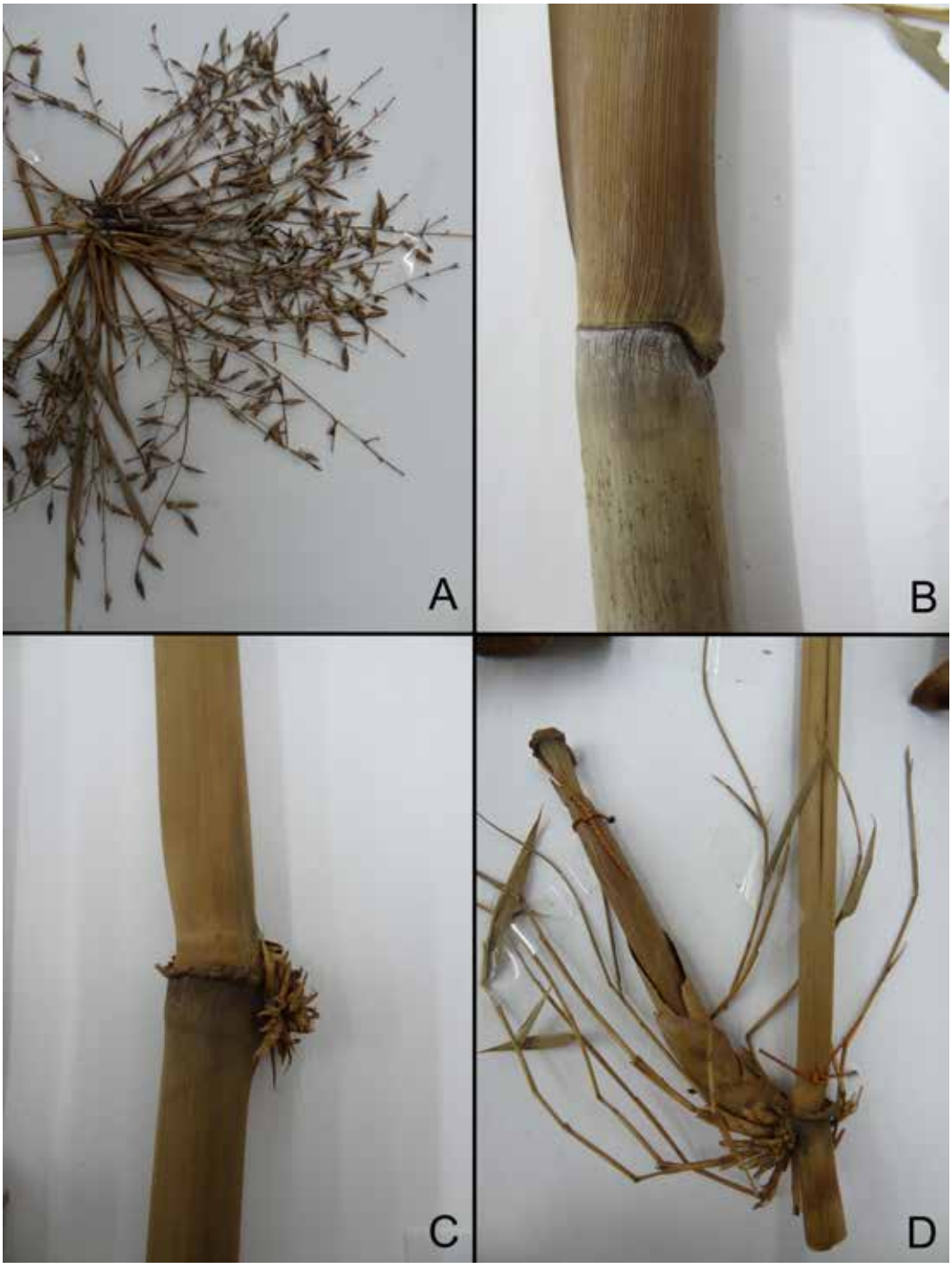

Fig. 10. *Widjajachloa* (Racemobambosinae) shows some typical characteristics of the subtribe: determinate inflorescences with ebracteate branches (**A**); a solitary culm bud (that, however, 'dips' below the nodal level compared to other genera of this subtribe) (**B**), development of a dominant primary branch axis that can be at first dormant and producing smaller, higher-order branches from its base (**C**), but later able to develop reiteratively (**D**) and replace or extend its parent axis. (Photos: K.M. Wong)

wrinkles. Foliage leaf sheaths with narrow and stiffly erect, horn-like auricles at the summit. Synflorescences in *Fimbribambusa* indeterminate (pseudospikelets), paniculate with very short branches, or in *Temburongia* 'determinate' or a reduced indeterminate condition (spikelets) (see comments below). Spikelets consisting of 1–3 glumes, 2–3 perfect (fertile) florets (in *Temburongia* only 1 rudimentary floret below the solitary perfect floret), and a rachilla extension bearing a terminal rudimentary floret. Palea keels wingless or very slightly winged. Stamens 6, filaments free. Ovary glabrous or hairy at the summit, with a short tissue-filled style; stigmas 3. Caryopsis basic.

(Fig. 11)

Distribution: Northwest Borneo, Philippines (Luzon Island), South Sulawesi, East Java, Lesser Sunda Islands (Alor), New Guinea.
Malesian genera: *Fimbribambusa* Widjaja, *Temburongia* S.Dransf. & K.M.Wong.
Comments: *Temburongia* has been consistently recovered as an independent lineage from Bambusinae and other clades (Goh et al. 2013). The molecular phylogenetic results of Chokthaweepanich (2014) demonstrate consistent clustering of the above two genera. Dransfield & Wong (1996) provide a detailed analysis of the inflorescence structure in *Temburongia*, noting solitary spikelets as well as sparse clusters of spikelets on the main inflorescence axis; the condition is best described as semelauctant although this could also be an intermediate condition with, or extreme reduction of, the iterauctant condition. Given the close alliance with *Fimbribambusa*, in which the inflorescence can bear proliferating clusters of a few to numerous pseudospikelets and is clearly iterauctant, we may interpret the condition in *Temburongia* inflorescences to be an extreme reduction of the iterauctant state.

TAXA OF UNCERTAIN SUBTRIBAL POSITION

Although *Ruhooglandia* S.Dransf. & K.M.Wong is distinct as a genus from *Chloothamnus* and *Widjajachloa* (Wong & Dransfield 2016), it has characteristics found in *Greslania* (Greslaniinae) and *Widjajachloa* (Racemobambosinae). Like *Greslania*, its inflorescence branches are subtended by well-developed prophylls or bracts, which are absent in the Racemobambosinae. On the other hand, like *Widjajachloa*, the sole perfect floret in its spikelet also has a significant rachilla extension bearing a rudimentary floret. *Ruhooglandia* has not been included in any phylogenetic assessment to date.

Recent molecular experiments (Goh et al., unpublished) show a number of aberrant *Racemobambos* species (*R. hirsuta* Holttum, *R. pairinii* K.M.Wong*, R. rigidifolia* Holttum, *R. setifera* Holttum) forming a cluster separate from typical *Racemobambos* (represented by the type *R. gibbsiae* and the allied *R. hepburnii* S.Dransf.). This group has a different branch complement organization from typical *Racemobambos*. The position of the extra-Malesian *Temochloa liliana* S.Dransf. (so far known only in Thailand) has yet to be clearly demonstrated in molecular experiments. Sungkaew et al. (2009) recovered *Temochloa* as an independent lineage external to the Bambusinae but did not have representatives of typical *Racemobambos*. The results of Kelchner et al. (2013) indicated non-clustering of *Temochloa* with typical *Racemobambos*.

Fig. 11. *Temburongia simplex* with typical characteristics of the Temburongiinae: development of a shelf-like patella around culm nodes (**A**), raised horn-like culm-leaf sheath auricles (**B**) and foliage leaf sheath auricles (**C**). (Photos: K.M. Wong)

* * * * *

I repeat my vow
in unchanging colors of
the ageless bamboo--
which still creates ten thousand
generations of shadows

Waka from 18th century Edo Japan attributed to poetess Gion Yuri (1694–1764), Stephen Addiss (1990)

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